

BODY TEMPERATURE AND SINGING IN THE KATYDID,
NEOCONOCEPHALUS ROBUSTUS (ORTHOPTERA,
TETTIGONIIDAE)

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Insects in the family Tettigoniidae produce sound by rubbing a sclerified ridge (plectrum) on the medial edge of the right forewing across a set of teeth (pars stridens) on the underside of the left forewing (Dumortier, 1964). The songs produced are composed of chirps, each chirp produced by a movement of the wings by one another. In some tettigoniids the chirp frequency is high enough that the sound produced appears continuous to a human listener (Pierce, 1948; Alexander, 1956). The frequency of wing movements and of chirps during singing in the katydid *Neoconocephalus robustus* is 150-200 per second (Josephson and Elder, 1968). One expects from this extraordinarily high frequency that the muscles moving the wings must have very high metabolic rates during singing, and that the thoracic temperature may rise well above the ambient temperature. The expectation of a high metabolic rate is in part confirmed by the structure of the wing muscles; the mitochondria in these muscles are large and numerous and comprise about 44% of the muscle fiber volume (Josephson and Elder, 1968). In this paper we will show that the thoracic temperature during singing is indeed considerably greater than the environmental temperature and that the katydid uses physiological and behavioral means to achieve elevated temperatures. Measurements of the thoracic temperature allow estimates of the metabolic cost of singing.

Heat production resulting from muscular activity and temperature regulation have been studied in a number of insects, usually in connection with flight and pre-flight warmup (Heath and Adans, 1967). *N. robustus* offers an unusually favorable preparation for examining temperature relations during intense muscular activity in an intact insect. The animals will sing spontaneously even when enclosed in a small container. Electrical measurements and temperature recordings can be made from an animal without resorting to either elaborate tethers or wind tunnels generally necessary to adequately study flying insects. Further the onset and cessation of singing are under the control of the animal rather than the experimenter as is often the case in flight experiments. The regulation of temperature by the regulation of activity is therefore a mechanism available to the animal.

MATERIALS AND METHODS

Adult specimens of *N. robustus* were collected from salt marshes in the vicinity of Woods Hole, Massachusetts. Only males sing and only males were used in these studies. The animals were kept in the laboratory under approximately

normal diurnal fluctuation in light intensity and were fed lettuce. Most animals sang spontaneously at or shortly after sundown each night. Males weigh 0.4–0.5 grams.

Muscle action potentials were recorded with 50 μ silver wires, insulated except at the tip. The electrodes were inserted into the desired muscles through small holes in the exoskeleton and were sealed in place with dental wax. The indifferent electrode was a bare silver wire in the abdomen. The electrode positions were verified by post-mortem dissection. Capacitor-coupled amplifiers were used to amplify the potentials which were then stored on magnetic tape for later photography and analysis. Both 40 gauge (0.2 mm) copper-constantan thermocouples and ultra-small thermistors (0.25 mm) were implanted in the thorax. Thermocouples were introduced through a hole punched in the pronotum and angled ventrally and posteriorly to lie within the mesothorax about 3 mm from the dorsal surface.

The animals were anesthetized with CO₂ while mounting recording electrodes and temperature transducers. Most animals did not sing in the evening following electrode and transducer implantation but they generally did on subsequent nights.

The thoracic temperatures were obtained from animals in the field and during behavioral studies by a specially constructed thermistor probe described by Heath (1967) and Heath and Adams (1969). Insects were captured in a net or grasped between the fingers by the posterior end of the elytra. The thermistor probe was punched through the dorsal surface to a depth of 4 mm. This probe has a thermal time constant of 0.2 sec. If the time between capture and measurement exceeded 5 seconds, the measurement was discarded because of the rapid heat loss from the insect.

RESULTS

Muscle activity during warm-up and song

Singing does not begin abruptly but is preceded by a period of muscle activity appropriately called warm-up, since it coincides with a noticeable rise in thoracic temperature. During warm-up the wings lie against the body and are not held in the slightly raised position taken during singing. There is little obvious movement of the thorax or wings during warm-up but the muscle activity is clear from electrical recordings of muscle action potentials. Initially the warm-up activity is discontinuous, occurring in bursts each several seconds long. These bursts become longer and more frequent and during late warm-up the activity is nearly continuous. There is usually a brief pause in muscle activity at the transition between warm-up and song.

Mortality was rather high in those animals implanted with both recording electrodes and a temperature transducer. Satisfactory records were obtained from only one animal. The results from this animal will be considered in some detail, however, since both the muscle activity and the thoracic temperature records are characteristic of all animals in which these parameters were measured independently. The action potential frequency from one of the forewing muscles of this animal during warm-up and singing is shown in Figure 1. During both late warm-up and singing the frequency of muscle action potentials is nearly constant

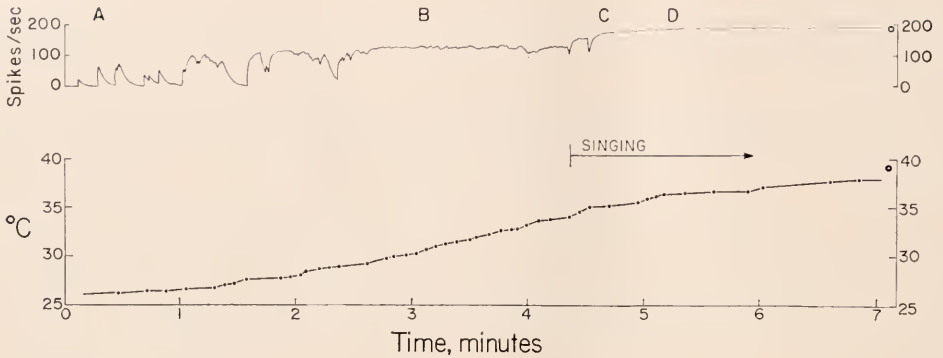


FIGURE 1. Muscle action potential frequency (right tergosternal muscle of the mesothorax) and thoracic temperature during warm-up and song. The recorded action potentials triggered a pulse generator whose output was fed into a leaky integrating circuit made with an operational amplifier. The triggering level was adjusted so that all large potentials, including the individual pulses in bursts triggered the pulse generator. The upper curve is the output of the integrator. Following a sudden change in pulse frequency the integrator output exponentially approaches an asymptote. The asymptotic value is a linear function of pulse frequency and the time constant of the approach is approximately 2 secs. The open circles at the right indicate spike frequency and thoracic temperature at the end of this singing period, approximately 4 minutes after the end of the records shown. The letters above the upper curve indicate the portions of the sequence from which the records of Figure 2 were taken.

even though the thoracic temperature steadily increases. This suggests that the pacemakers which generate the action potential patterns may be located in some part of the animal which does not undergo the large temperature changes seen among the musculature of the mesothorax.

Some details of the muscle electrical activity are seen in Figure 2. During singing the action potentials in the two recording channels are out of phase (Fig. 2D) indicating that the muscles, the right subalar and tergosternal, are antagonists during singing. At the onset of singing the tergosternal (lower channel) sporadically failed to fire for one or sometimes several consecutive cycles (Fig. 2C). This skipping of occasional cycles gives an opportunity to examine electrical interactions between the recording channels. Because of the small size of the thorax and the relatively large volume of the active muscles, electrical isolation between recording channels is necessarily incomplete. Some part of the signal recorded with extra-cellular electrodes in one muscle is inescapably due to activity in surrounding muscles. During missed cycles the record from the tergosternal muscle shows a small deflection coincident with the action potential from the subalar (Fig. 2E). This represents pickup from the subalar and its synergists. In *N. robustus* synergistic muscles fire essentially synchronously during singing. This could hardly be otherwise, given that the whole wing movement cycle is completed within 5–6 msec. In skipped cycles there is no deflection in either the tergosternal or the subalar records at the expected time of tergosternal firing. This suggests that not only the right tergosternal muscle but also all or most of its synergists have not fired; otherwise, one would expect to see electrical events generated by adjacent muscles in the records at this time. There is some

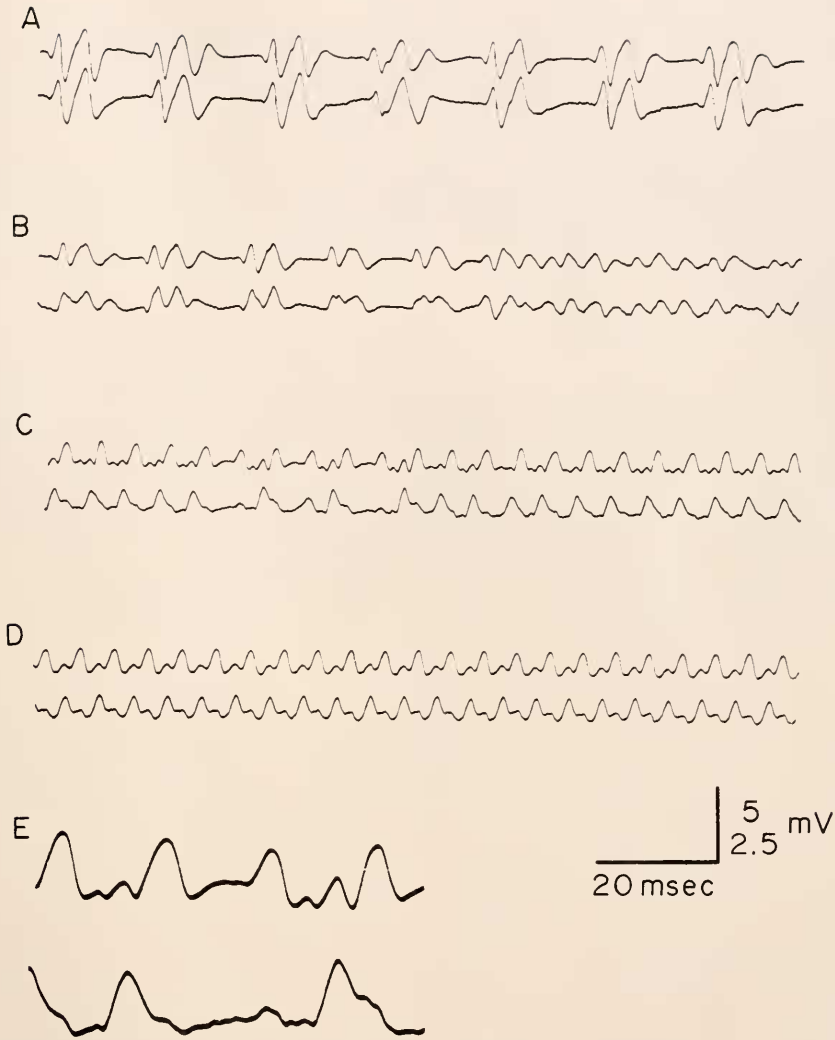


FIGURE 2. Action potentials from the right subalar (upper channel) and the right tergosternal (lower channel) muscles of the mesothorax. A portion of C, including a cycle in which the tergosternal failed to fire, is enlarged 3 times in E. The calibration applies to A-D.

pickup from antagonistic muscles in each channel, but the major deflections are clearly produced by the muscle from which the recording is made with possible contributions from its synergists.

During early warm-up, potentials in each channel are essentially synchronous. Since electrical coupling between recordings from antagonistic muscles has been shown to be small, this indicates that muscles which are antagonists during singing contract simultaneously during warm-up. Similar multichannel recordings from

other animals indicate that muscles synergistic during singing maintain their synchrony during warm-up as well. Thus, during warm-up there is synchronous activity among a number of the forewing muscles. Since the active muscles include a number of antagonistic elements the resultant is heat production with little overt movement.

During early warm-up the muscle action potentials usually occur as pairs or short bursts of pulses. The interval between adjacent pulses can be quite short. The average interval between the peaks of the pulse pairs of Figure 2A is only 4.3 msec. During later warm-up the muscle activity becomes faster but less regular (Fig. 2B).

Body temperature during activity

Eight males were implanted with thermocouples and their thoracic temperature monitored for 3–5 successive nights. Figure 3 shows a sequence of warm-up and singing for a single male.

Activity begins with a period of warm-up. The increase in temperature during warm-up is approximately linear. Toward the end of the warm-up period the rate of warming may decline. When singing begins, the rate of warming is further decreased. During the singing period the body temperature may rise an additional increment. When singing stops, the body temperature falls rapidly along a Newtonian course back to ambient temperature.

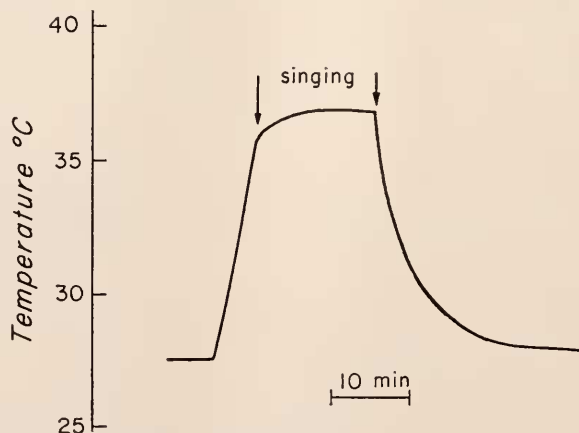


FIGURE 3. Thoracic temperature during a singing period of *N. robustus*. Air temperature was 27.5° C.

Warm-up. The rate of rise of thoracic temperature is nearly constant for a given warm-up period. It varies from 0.94° C/min to 2.20° C/min. Thirty warm-ups from eight animals averaged 1.54° C/min (\pm S.D. 0.33). These periods occurred at ambient temperatures from 22.5° C to 29° C.

Singing. Animals in the laboratory began singing at an average thoracic temperature of 33.5° C (S.D. 1.48; N = 23). The thoracic temperature at the onset of singing increased with air temperature 0.65° C/°C over the range 23.5°–

29° C. The lowest thoracic temperature at which singing began was 30.5° C, which occurred at ambient temperatures of 27.6° C and 28.5° C.

During singing thoracic temperature rises by about 1° C, reaching an average temperature of 34.4° C (S.D. 2.25; N = 30). The maximum thoracic temperature during singing increases with increasing ambient temperature. A linear regression fitted to data collected in the laboratory had a slope (thoracic temperature/ambient temperature) of 0.60° C/°C over the temperature range 22.5–29.5° C (Fig. 4). Katydid singing at air temperature of 16.8° C–22° C in the field are also shown in Figure 4. The linear regression fitted to the laboratory data seems to fit the field measurements. This katydid may be unable to sing at thoracic temperatures below about 28° C.

Singing period. *Neoconocephalus robustus* sings readily in the laboratory for a period of up to an hour even when implanted. In the field this katydid sings continuously for extended periods. Table I shows the characteristics of the song recorded during several evenings near Falmouth, Massachusetts in August, 1968. On subsequent evenings we found *N. robustus* singing at air temperatures as low as 16.8° C and also as late as 10:00 PM (EST).

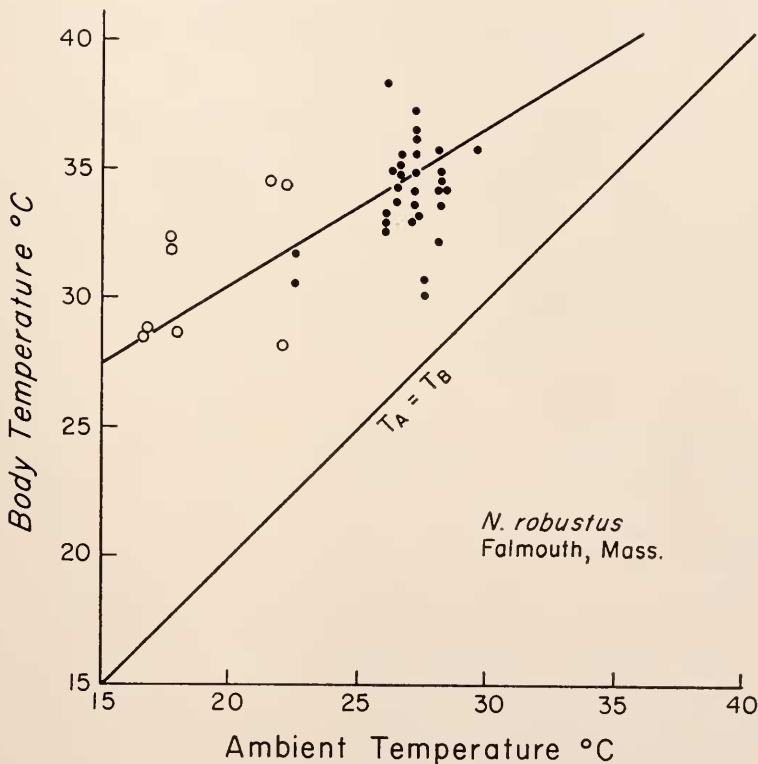


FIGURE 4. Thoracic temperature of singing katydids plotted against air temperature at the time of singing. A linear regression fitted to points from animals measured in the laboratory, fits field measurements, \circ , equally well.

TABLE I
Duration and conditions during singing activity by *N. robustus*

Animal	Range of call duration	Sum of call periods	(N) calls	Time EST	Date	Air temp °C
A	37''- 9'27''	38'26''	7	7:06-10:05	8/13	—
B	5'00''-51'42''	70'09''	5	7:13- 8:23	8/15	21°
C	9'59''-32'37''	53'45''	3	7:38- 8:39	8/15	21°
D	39'26''	39'26''	1	8:01- 8:40	8/23	23°
E	3'00''-68'19''	80'11''	4	7:20- 8:45	8/23	23°
\bar{X}	37''-68'19''	56'25''	20			

Cooling. At the end of an active period the thoracic temperature returns to ambient levels. The cooling rate is approximately linear with temperature gradient and is thus passive or Newtonian (Fig. 5). The cooling curve can be used to estimate heat loss in a given gradient or heat production if the body temperature is constant.

Behavioral studies

This phase of the study was intended to determine the thermal limits of activity and to locate reliable behavioral estimates of the temperature tolerance

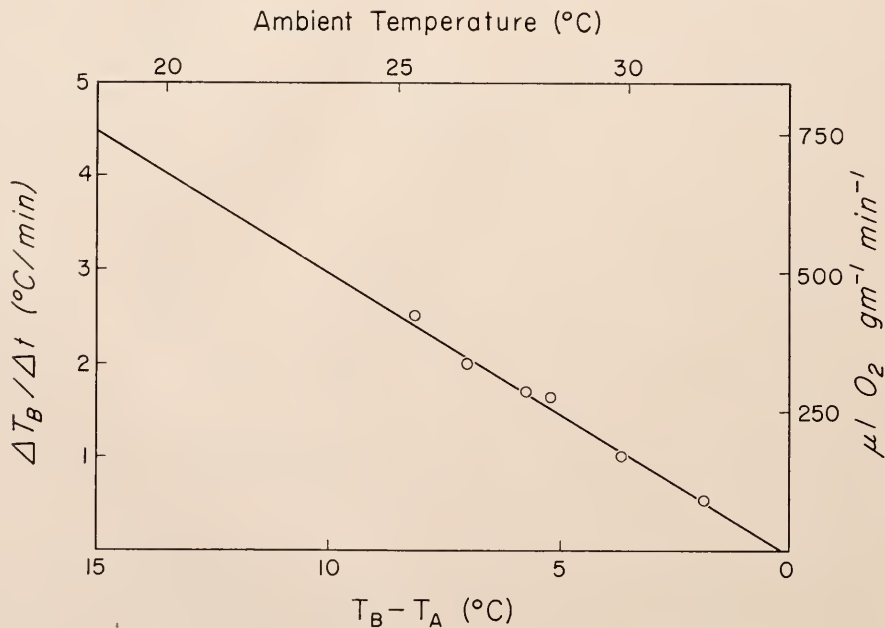


FIGURE 5. Cooling curve of the thorax plotted as a rate of change of temperature (left axis) against gradient (bottom axis). A line passing through zero is fitted by eye to the points. If the insect maintains a thoracic temperature of 33.5° during singing and temperature change is converted to heat production (right axis), then the line is an estimate of the expense of singing at decreasing ambient temperatures (upper axis). (See discussion for further explanation.)

of this animal. In each case, males captured in the field, in the evening, were brought into the laboratory and investigated the next day.

Response to cold. Individual males were cooled in beakers immersed in an ice bath until immobilized. They were then removed to room temperature ($\sim 25^{\circ}\text{C}$), and allowed to warm.

As the insects warmed, responsiveness returned. When the insect could right itself, its thoracic temperature was quickly recorded. This response appeared at an average body temperature of 21.8°C (Table II). This is an unexpectedly high value since individuals in nature sing at lower air temperatures. Some individuals retain awkward and limited motor activity during cooling to as low as 11°C , but once immobilized motor control does not reappear during warming until 21°C is reached.

TABLE II
Behavioral responses to temperature in Neoconocephalus robustus

Response	Mean ($^{\circ}\text{C}$) (S. D.)	Range ($^{\circ}\text{C}$)	N.
Righting	21.8 (1.24)	19.5-23.5	10
Voluntary flight	33.7 (2.30)	29.0-35.2	5
Shade-seeking	37.6 (1.60)	35.0-40.0	10
Loss of motor control	43.9 (0.64)	42.5-44.5	10

Response to heat. Individual males were heated in pasteboard containers held under a 250 watt infra-red heat lamp until they lost motor control. They were then quickly removed and the thoracic temperature recorded.

The loss of motor control occurs at an average temperature of 43.9°C (Table II). This temperature is an ecological lethal point because individuals in nature would be unable to avoid further increases in body temperature by seeking cooler locations once this level is passed. All individuals regained control upon cooling, but two of twelve individuals treated in this manner died within 24 hours.

Maximum voluntary tolerance

Individuals in the previous experiment became exceptionally active during the later stages of heating. This activity is equivalent to the behavioral response of heat avoidance or shade-seeking. Insects in the field periodically are exposed to the direct rays of the sun. Insects typically retreat from these positions either upon first contact with direct irradiation or at a closely regulated temperature level after some minutes of exposure (Heath, 1969a). *Neoconocephalus robustus* follows the latter course.

To determine the temperature level of this response, individuals were placed on a segment of pine branch 18 cm below 250 watt IR lamp. The animals warmed for several minutes then shifted to a shaded position beneath the branch. They were then quickly retrieved and thoracic temperatures measured. These movements occurred at average thoracic temperatures of 37.6°C (Table II).

During the warming *N. robustus* takes up basking positions maximizing the surface area presented to the radiant source. If the insect is replaced on the

branch in a shaded position following measurement it returns shortly to a fully exposed position beneath the lamp. Ultimately it takes up a partially exposed position on the branch and remains indefinitely at or slightly below the temperature of shade-seeking. The persistence of these patterns is strong evidence that during the daylight hours, *N. robustus* regulates its body temperature behaviorally to the same range of temperature that males achieve in the evening while singing.

A few individuals flew rather than moved to shade. This response appeared at 33.7° C (Table II). Attempts to force flight by throwing individuals into the air at ambient temperatures of 20°–30° were unsuccessful.

DISCUSSION

The katydid, *Neoconocephalus robustus* has a very distinctive and intensive song. The song is generated by wing movements driven by muscles at an exceptionally high frequency. During singing this insect not only generates enough heat to raise the thoracic temperature well above ambient but it may depend upon reaching an elevated temperature in order to achieve the wing frequency necessary for its song. It precedes singing with a period of warm-up during which it contracts the thoracic muscles without significant movement. This is accomplished by firing antagonist muscles synchronously. The only product of this activity is heat which causes the thoracic temperature to rise. The pattern of muscular activity changes abruptly when an elevated thoracic temperature is reached and singing begins.

Heat production due to muscular exertion is well known among insects (Sotovalta, 1954). The locust, *Schistocerca gregaria*, may warm 6° C during flight (Weis-Fogh, 1952). The cicada, *Magicicada septendecem*, may sustain a 2–6° increment above ambient temperature by intermittent flight (Heath, 1968b). In neither case do they seem to depend or capitalize on this heat production in normal activity. On the other hand, some insects, notably bees and moths use the heat generated by flight to maintain relatively constant thoracic temperatures during activity (Esch, 1968; Heath and Adams, 1967). In the case of moths a period of warm-up precedes flight. As in the katydid, antagonist muscles contract synchronously yielding little movement but high heat production (Kammer, 1968; McCrea, 1969). Both bees and moths are conspicuously insulated to retard heat loss (Church, 1960), and among moths the suite of behavioral, physiological and morphological adaptations permit these animals a degree of independence of environmental conditions of significance to a nocturnal animal.

The katydid, *N. robustus*, is intermediate between passive heat producers like the locust and active endothermic insects like the moth. The katydid lacks an insulative layer to retard heat loss. It also is more sensitive to ambient temperature during heat generating activity than moths. Over the range of ambient temperatures it is likely to encounter in nature (15°–30°), its thoracic temperature during singing shows a positive regression with ambient temperature of 0.6° C/°C. Moths over the same range are independent of air temperature (Heath & Adams, 1967). Apparently, katydids depend on heat production only for singing while many moths feed, seek mates, lay eggs only when the body temperature is regulated to a controlled range (Heath and Adams, 1967). The katydid does

not depend upon internal heat production during feeding, mating and egg laying. On the other hand, *N. robustus* like many diurnal insects will bask readily when presented with a source of radiant energy. Its behavior predicts that during daylight hours it conducts its activities over a range of body temperatures similar to those achieved by singing. Figure 6 summarizes the thermal responses of *N. robustus*.

Both the rapidity of the muscle activity and the large gradient maintained between the thorax and surroundings predict that the male katydid must expend energy at an extraordinary rate during singing. During a singing period the body temperature remains relatively constant, which means that the heat produced just balances the heat lost. That portion of the muscular activity that produces heat at a given gradient to the environment can be estimated exactly as the rate the body cools through the same gradient.

If heat production during cooling is small compared to heat loss, if the convective flow about the singing insect is disregarded and if the singing process is inefficient (*i.e.*, most of the expended energy appears as heat rather than sound), then analysis of the cooling curve of this insect can be used to estimate the cost of singing.

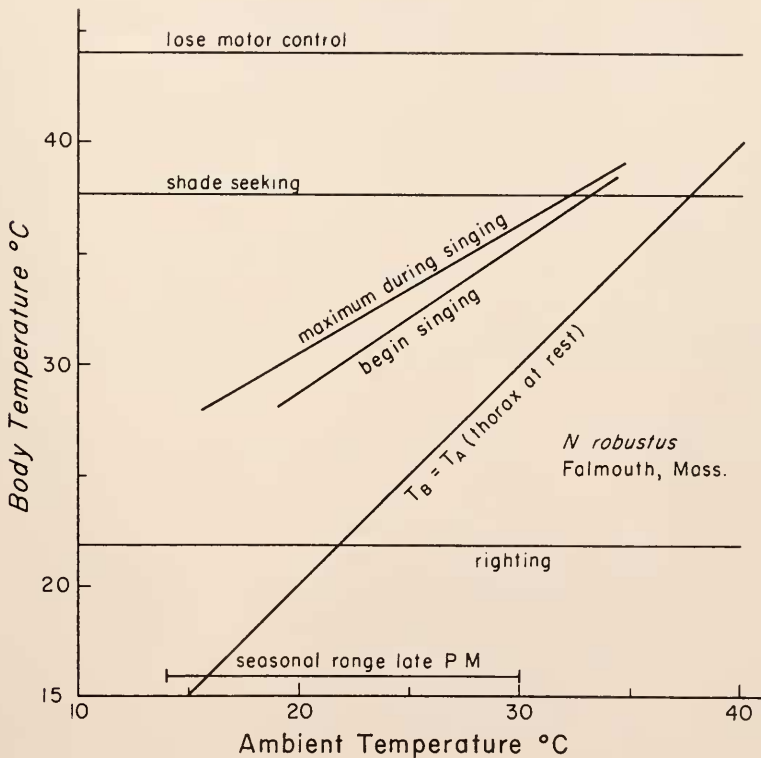


FIGURE 6. Summary of the temperature responses and states of *N. robustus*. The responses are explained in text. A bar representing the air temperatures ordinarily encountered during the singing season in the field is shown at the bottom of the graph.

It has been shown that the metabolic rate during flight of insects is often 100 times that of the resting rate (Prosser and Brown, 1961). Hence, heat production during cooling should be very small. The singing katydid does generate a flow of air about the thorax which is not present in the quiet insect. Hence, the cooling curve will underestimate heat production of singing. Similarly, the cooling curve will also underestimate the energy dissipated as sound and kinetic transfer during singing. It is unlikely that the katydid is more than 10–15% efficient. Heath and Adams (1967) showed that metabolic rate during activity in sphinx moths exceeded the rate calculated from the cooling curve by about 15%. Hence, the cooling curve can be used to make a conservative estimate of metabolic rate in singing.

The rate of temperature change with time for an object such as an insect's thorax which produces heat internally and loses it to the environment is given by the following:

$$\frac{dT_B}{dt} = \frac{1}{WS} \left(\frac{dHp}{dt} - \frac{dHl}{dt} \right) \quad (1)$$

$$\frac{dT_B}{dt} = \text{rate of change in body temperature (deg/sec)}$$

W = mass of object (g)

S = specific heat of object (cal/g deg)

$$\frac{dHp}{dt} = \text{rate of heat production (cal/sec)}$$

$$\frac{dHl}{dt} = \text{rate of heat loss (cal/sec)}$$

If it is assumed that heat loss is due entirely to conduction from the object's surface to the environment, the rate of heat loss is given by Newton's law of cooling:

$$\frac{dHl}{dt} = AC(T_B - T_A) \quad (2)$$

A = surface area of object (cm²)

C = thermal conductance of the surface (cal/deg sec cm²)

T_B = body temperature (deg)

T_A = environmental temperature (deg)

Solving (1) for the rate of heat production and substituting (2) for the rate of heat loss gives:

$$\frac{dHp}{dt} = WS \frac{dT_B}{dt} + AC(T_b - T_a) \quad (3)$$

At the cessation of singing heat production is presumably negligibly small. Under these conditions, when dHp/dt is essentially zero, equations (1) and (3) can be rewritten as:

$$\frac{dHA}{dt} = -WS \frac{dT_B}{dt} \quad (4)$$

$$\frac{dT_{B_A}}{dt} = \frac{AC}{-WS} (T_B - T_A) \quad (5)$$

From (5) the rate of cooling at the cessation of singing is a linear function of the temperature gradient between the animal and its environment. In Figure 5 this is plotted for an animal of known weight using the method of Heath and Adams (1969). A line intersecting zero gradient was fitted by eye to the points. Using thoracic weight and assuming a specific heat of 0.8 for insect tissue (Krogh and Zeuthen, 1941) the heat loss for each gradient is readily calculated from equation (4) (Table III). This value equals the heat production necessary to maintain the same gradient. These were converted to the more familiar measurement of weight-specific oxygen consumption by assuming a caloric equivalent of oxygen of 4.8 cal/ml O_2 . The high metabolic rate predicted by these calculations is consistent with both the muscular activity and poor insulation. For an animal to maintain a temperature gradient of 15° C between its thorax and the environment it must produce approximately 0.5 cal/min which is equivalent to an oxygen consumption of 0.1 ml O_2 /min or, for a 0.14 g thorax, 0.75 ml O_2 /g thorax wt/min. This is similar to the O_2 consumption values reported for actively flying insects which range from 0.17 to 1.5 ml O_2 /g body weight/min (Prosser, 1961).

Another means of dramatizing the turnover of energy in a singing katydid is to estimate the rate of disappearance of metabolites with activity. If we assume a 15° C gradient, a singing *N. robustus* would expend about 30.6 cal/hr. This would require 0.0032 g of fat at 9500 cal/g. At a total weight of 0.4 g, *N. robustus* metabolizes 0.80% of its body wet weight in one hour of singing (or, assuming a water content of 80%, 4% of its dry weight). These figures underestimate expended energy, because some energy appears as sound and movement of the wings.

During much of warm-up and during singing the body temperature increases approximately linearly with time. When rate of rise of body temperature and

TABLE III
Energy expenditure of *N. robustus* during singing

$T_B - T_A$	cal/min*	cc O_2 /g/min*	Fat consumption		
			g/hr	% wet body wt**	% dry body wt**
5°	0.17	0.25	0.0011	0.27	1.4
10°	0.34	0.50	0.0021	0.53	2.9
15°	0.51	0.75	0.0032	0.80	4.0

* Heat production by thorax only (0.14 g).

** % Total body wt (0.40 g wet; 0.08 g dry).

the ambient temperature are constant, the rate of heat production is a linear function of the body temperature (equation 3). During late warm-up and early singing, when the body temperature is linearly rising and hence the rate of heat production increasing, the frequency of muscle contractions is nearly constant for long periods. Thus it appears that the amount of heat liberated by each contraction increases as the body temperature increases. The muscle action potentials give no indication of increasing recruitment of muscles or units within muscles with increasing thoracic temperature so the greater heat production probably reflects greater energy release by the same population of muscle fibers. The duration of the twitch initiated by each action potential presumably becomes shorter as the thoracic temperature increases (*cf.* Neville and Weis-Fogh, 1963). The rate at which energy is released during a twitch must therefore have a rather high temperature coefficient for the heat production per contraction to increase in the face of shortening twitch duration.

N. robustus by the mechanism cited generates a distinctive song at considerable expense. The cost of the song is met perhaps because of competitive interaction with another species of *Neoconocephalus* in nearly the same habitat. In the study area *N. robustus* overlaps broadly with *N. ensiger*. The two species are very similar in appearance, but *N. ensiger* powers its rather soft intermittent song by much slower muscles (10–15 cps). Among tettigoniids song distinctiveness is strongly selected. Some insight into this might be derived by careful comparative cost analysis of *N. ensiger* and *N. robustus* song.

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SUMMARY

1. The katydid, *Neoconocephalus robustus*, produces a continuous song by rubbing its forewings together at frequencies of 150–200 per second. During singing the thoracic temperature is 5–15° C higher than that of the environment, the temperature gradient being greater the lower the ambient temperature.

2. Singing is preceded by a warm-up period during which normally antagonistic forewing muscles contract synchronously. The result is heat production and a rising thoracic temperature (1.5° C/min) with little overt movement.

3. The thoracic temperature at the onset of singing averages 33.5° C at ambient temperatures at 23.5°–29° C.

4. The rate of heat loss at the cessation of singing indicates that the animal must produce 0.5 cal/min (3.6 cal/min/g thorax weight) to maintain a 15° C temperature gradient.

5. This insect is immobilized by cooling to 11° C, but regains mobility when rewarmed to 21.5° C. It is reversibly immobilized at thoracic temperatures above 43.9° C.

6. *N. robustus* basks readily, but moves to shade at body temperatures of 37.6° C. Shuttling between sunlight and shade would permit this insect to regulate

its body temperature to a high but restricted temperature range during daylight hours.

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